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REVISIONARY STUDY OF THE GENUS *ALLIONIA* (NYCTAGINACEAE)

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ABSTRACT

Allionia is a genus with two widespread partially sympatric species, *A. choisyi* and *A. incarnata*. Both occur throughout the warmer more xeric regions of North and South America and are abundantly represented in herbaria. *Allionia choisyi* does not appear to have meaningful morphogeographical infraspecific categories in either North or South America. *Allionia incarnata*, however, appears to have three well-marked but intergrading morphogeographical infraspecific taxa in North America: var. *incarnata*, a widespread weedy taxon primarily centered in North America but extending into South America; var. *nudata* (Standl.) Munz, largely confined to the Sonoran desert regions of México and closely adjacent U.S.A. (southern California, southern Nevada, and southwestern Arizona); and var. villosa (Standl.) B.L. Turner, *comb. nov.*, largely confined to the intermontane region of Nevada and Utah southwards to northern México. Keys to the taxa are provided along with maps showing their distribution.

KEY WORDS: Nyctaginaceae, *Allionia*, taxonomy

Allionia, as treated here, is a genus of only two widespread sympatric species, one for which (*A. incarnata*) various infraspecific categories have been proposed. The genus has had a checkered nomenclatural history, some of the early workers (*e.g.*, Standley 1918) incorrectly took up the generic name *Wedelia* Loefl. (not *Wedelia* Jacq.) for its members, but its correct name is *Allionia* L., first proposed by Linnaeus in 1759 and typified by material of *Allionia incarnata* from the coastal region of Venezuela (near Cumana).

Most workers have recognized two or three species in the genus, these largely circumscribed by fruit characters, but at least one worker (*e.g.*, Rzedowski 1981, *cf.* discussion under *Allionia choisyi*) has recognized only a single species in the complex.

The present account is based upon the examination of approximately 1,000 herbarium specimens housed at the following institutions: ARIZ, F, GH, LL, NY, TEX, UC, US. The distributional maps (Figure 1) are based upon these collections, all of which have been annotated and serve as documentation for the study.

ALLIONIA L.

Wedelia Loefl. 1766, not *Wedelia* Jacq. 1760.

Wedeliella Cockerell.

Annual or perennial, mostly prostrate or recumbent dichotomously branching herbs, the stems arising from slender or enlarged ligneous tap roots. Leaves opposite, simple, unequal in size. Flowers perfect in axillary paniculate clusters of 3, the clusters subtended by bracts that persist and enclose the 3 fruits. Perianth in only 1 series, funnelform to rotate, pink to lavender. Stamens 4-8. Stigmas capitate. Anthocarps (fruits) with ventral (inner) surfaces rounded to flattened, the dorsal side glandular, rounded and incurved to broadly flattened, the margins with 2-8 broad to narrow teeth. Seeds with uncinate embryos.

Type species, *Allionia incarnata* L.

A widespread weedy genus with only two species, both of these partially sympatric in the drier regions of North and South America.

KEY TO SPECIES

1. Anthocarps (fruits) with ventral (inner) surfaces decidedly rounded, the dorsal side with usually 2-4 incurved deltoid to narrowly triangular teeth; stems procumbent; roots strongly perennial. ..... *A. incarnata*

1. Anthocarps with ventral surfaces decidedly flattened, the dorsal side with usually 5-8 flattened linear-lanceolate teeth; stems strictly prostrate; roots annual or weakly perennial, sometimes strongly perennial. ..... *A. choisyi*

ALLIONIA CHOISYI Standl.

Allionia incarnata L. var. *glabra* Choisy *in* DC., *Prodr.* 11:435. 1849. *Wedelia glabra* (Choisy) Standl., Contr. U.S. Natl. Herb. 12:332. 1909. *Wedeliella glabra* (Standl.) Cockerell, Torreya 9:167. 1909. *Allionia glabra* (Choisy) Standl., Field Mus. Publ. Bot. 8:10. 1930.

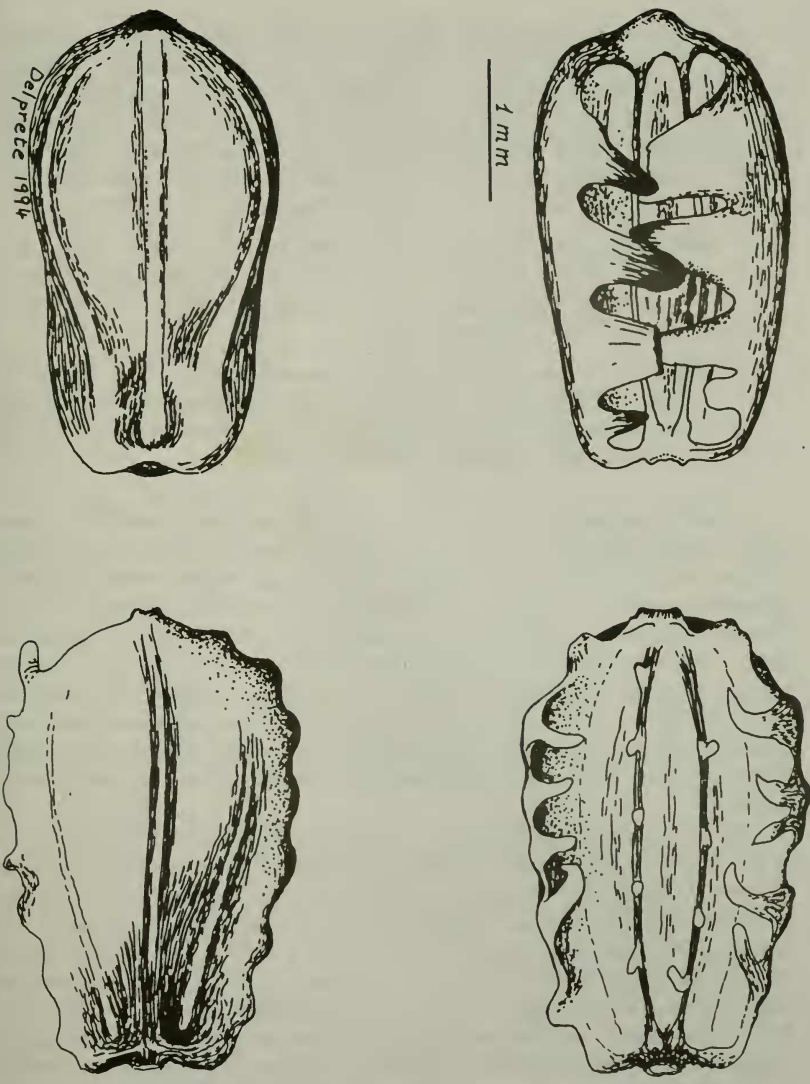

Figure 1. Fruits (anthocarps) of *Allionia choisyi* (to left) from isotype (GH) and *A. incarnata* var. *incarnata* (to right) from Perú, South America (*Dillon 3215* [TEX]).

Not *Allionia glabra* (S. Wats.) O. Kuntze ≡ *Allionia choisyi* Standl., Field Mus. Publ. Bot. 8:310. 1931. TYPE: MEXICO. Tamaulipas: San Fernando, w/o date, *Berlandier 816* (pl. exs. *2236*) (LECTOTYPE [selected here]: Bernhardi Herb., G-DC; Isolectotype: GH!). In his original description Choisy cited two specimens, both collected by Berlandier, one from the environs of México City (exs. *577*) and one from San Fernando, Tamaulipas (exs. *2236*).

Allionia incarnata L. forma *multiserrata* Heimerl *in* Urban, *Symb. Ant.* 7:212. 1912. TYPE: HAITI. "Prope Poste Coudan inter sexa ruderalia", 100 m, Jan w/o year, *Buch 643* (LECTOTYPE [selected here]: GZU; Isolectotype: NY!).

Allionia incarnata L. forma *glutinosissima* Heimerl, Rep. Spec. 31:97. 1939. TYPE: U.S.A. Arizona: Cochise Co., Paradise, outwash soil, camp ground, 5500 ft, 2 Oct 1907, *J.C. Blumer 1695* (HOLOTYPE: B, destroyed?; Isotypes: ARIZ!,GH!,NY!).

Annual (seemingly) or perennial herbs with markedly prostrate stems. Stems mostly slender, puberulous to puberulopilose. Larger leaves mostly 2-5 cm long, 1.2-3.5 cm wide; petioles 1-2 cm long; blades ovate to elliptic, sparsely pubescent to glabrate, the margins ± crenulate. Flowers axillary, their pedicels slender, mostly 0.5-1.5 cm long, but often shorter. Involucral bracts ovate, mostly 3-5 mm long. Perianth mostly 3-6 mm high, pink to purple. Stamens 4-6, mostly included, 3-4 mm long. Fruits 3-5 mm long, 3-4 mm wide, flattened, the abaxial surfaces with 5-8 sharp, appressed, narrowly triangular teeth (rarely gland-tipped) along each margin, between these occur 2 rows of sticky glandular protuberances that readily adhere to the enclosing bracts.

Allionia choisyi is sympatric with *A. incarnata* (Figure 3). Vegetatively it is difficult to distinguish between these, but their fruits are markedly different, as shown in Figure 1. It is tempting to view the two taxa as but fruit forms, so similar are their habits. Standley (1909), however, took *A. choisyi* to be an annual, at least as the species occurs in "New Mexico and in other places from which I have examined specimens with roots ...". My own observations bear this out for the region concerned, but numerous plants from elsewhere having the characteristic flattened fruits of *A. choisyi* show strongly developed, apparently perennial rootstocks. *Allionia choisyi* mostly occurs in loose sandy soils while *A. incarnata* occurs in clay or silty-clay substrates, to judge from label data.

As noted under *Allionia incarnata*, Rzedowski (1951) thought *A. choisyi* to be inseparable from that species, but like most workers who have treated the two taxa, I find these to be "clear-cut" species based upon characters of the fruit; only rarely have specimens with the two fruit types been collected

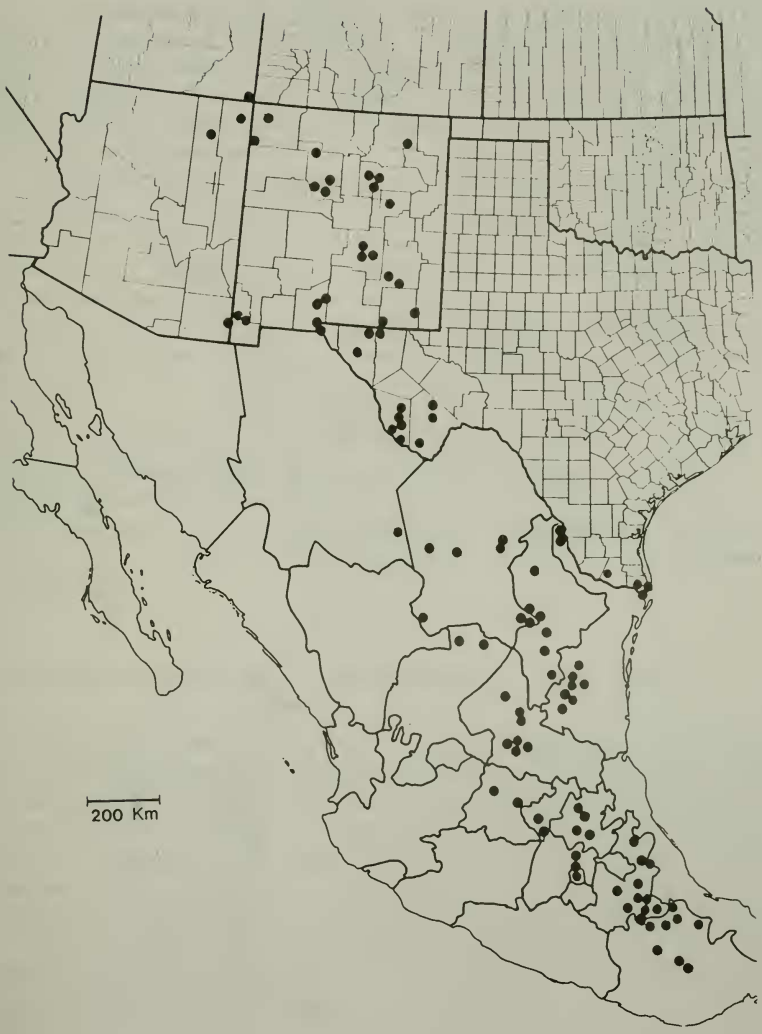

Figure 2. Distribution of *Allionia choisyi* in México and U.S.A.

Figure 3. Distribution of *Allionia choisyi* (diagonal lines and open circles) and *A. incarnata* (clear area and closed circles).

together at the same site (*e.g.*, U.S.A. Arizona, Cochise Co., Paradise, *Blumer 1695* [*A. choisyi*] and *Blumer 1694* [*A. incarnata*]) in which case they were readily viewed as distinct by their collectors, Blumer noting that *A. choisyi* "Hugs the ground more closely than [number] 1694 with which it grows". From among the many sheets of both species which I examined truly intermediate fruits were never encountered.

Allionia incarnata f. *glutinosissima* is a small-fruited form in which the marginal teeth are gland-tipped. It occurs in an area where three taxa are known to occur within close proximity: *A. incarnata* var. *incarnata*; *A. i.* var. *villosa*, and *A. choisyi*. Perhaps complex hybridization between two or more of these taxa has produced this rather bizarre form.

Plants similar to f. *glutinosissima* occur sporadically elsewhere (*e.g.*, vicinity of Albuquerque, New Mexico, *Rose 17800* (US) (the specimen mounted on the same sheet with a collection of *Allionia incarnata*). It is tempting to consider (in such instances) the possibility that marginal teeth with glands arise in situations of complex hybridization; alternatively *A. choisyi* might occasionally produce oddly glutinous fruit forms, throughout its range, there being a tendency for its fruits to be more glutinous than *A. incarnata*.

An excellent illustration of *Allionia choisyi* showing fruits can be found in Fay's (1980) treatment of *Allionia* for the Flora of Veracruz, albeit labeled as *A. incarnata* L.

ALLIONIA INCARNATA L., *Syst. Naturae*, ed. 10, 2:90. 1759.

Perennial herbs with procumbent or trailing stems. Stems slender or robust, variously pubescent (puberulous to villous to nearly glabrous). Larger leaves mostly 2-8 cm long, 1.5-4.5 cm wide; petioles 1-4 cm long; blades ovate or oval to obovate, variously pubescent to glabrate, the margins crenulate or undulate. Flowers axillary, their pedicels 0.5-4.0 cm long, rarely ± sessile. Perianth mostly 4-15 mm high, pink to purple. Stamens 5-8, 4-20 mm long, mostly exserted or nearly so. Fruits 4-6 mm long, 2-3 mm wide, the adaxial portion rounded (rarely weakly so), the marginal teeth 3-4(-5), usually obtuse, rounded or nearly absent (between these 2 rows of sessile glutinous glands, rarely the glands absent).

KEY TO VARIETIES

1. Perianth mostly 8-15 mm long, at anthesis 10-20 mm across; mostly mid-elevational regions of the North American Sonoran desert west of the Continental Divide. ..... var. *villosa*

1. Perianth mostly 4-8(-10) mm long, at anthesis 8-10(-12) mm across; widespread, in the U.S.A. mostly mid-elevational regions east of the Continental Divide or else in lower elevational zones of Sonoran desert regions. ..... (2)

   2. Anthocarps mostly 3-4 mm long; involucres mostly 4-5 mm long; Sonoran desert regions, Baja California, Sonora and closely adjacent U.S.A. ..... var. *nudata*

   2. Anthocarps mostly 4-5 mm long; involucres mostly (4-)5-7 mm long; widespread in North America mostly occurring in the Chihuahuan desert regions east of the Continental Divide southward to Hidalgo, México, also in South America. ..... var. *incarnata*

ALLIONIA INCARNATA L. var. *INCARNATA Allionia incarnata* L., *Syst. Naturae*, ed. 10, 2:90. 1759. *Wedelia incarnata* (L.) Kuntze, *Rev. Gen. Pl.* 533. 1891. *Wedeliella incarnata* (L.) Cockerell, Torreya 9:167. 1909. TYPE: VENEZUELA. Sucre: near Cumana, 1754, *Loefling s.n.* (HOLOTYPE: LINN).

Wedelia cristata Standl., Contr. U.S. Natl. Herb. 12:331. 1909. *Wedeliella cristata* (Standl.) Cockerell, Torreya 9:167. 1909. *Allionia cristata* (Standl.) Standl., Field Mus. Publ. Bot. 8:310. 1931. TYPE: U.S.A. Arizona: Navajo Co., Holbrook, 15 Jul 1896, *Myrtle Zuck s.n.* (HOLOTYPE: US; Isotypes: NY!,US!).

Wedelia incarnata (L.) Kuntze subsp. *anodonta* Standl., Contr. U.S. Natl. Herb. 12:332. 1909. *Wedeliella incarnata* (L.) Cockerell var. *anodonta* (Standl.) Cockerell, Torreya 9:167. 1909. TYPE: U.S.A. New Mexico: "plains of western New Mexico", Jul 1880, *Rusby 355* (HOLOTYPE: F!).

As shown in Figure 2, this is a widespread taxon in North America occurring from northern New Mexico southward throughout most of northcentral Mexico. It is also highly variable and I have been unable to distinguish North American collections from South American collections. *Allionia i.* var. *incarnata* is sympatric with *A. choisyi* in both North and South America (Figure 2). *Allionia choisyi* is readily distinguished from *A. incarnata* by its dorsally flattened anthocarps which usually possess 4-6 flattened marginal dentations, the latter mostly narrowly acute (vs. anthocarps rounded dorsally with 3-4 obtuse or rounded dentations). Nevertheless, occasional anthocarps of an intermediate nature suggest that the rare hybrid between these might occur, but I have not examined collections where the two taxa occur together with putative hybrids. According to Dr. James Henrickson (pers. comm.) populations

of *A. choisyi* from northern México are reasonably uniform morphologically, appearing quite different from those of *A. incarnata*, both in habit, flower size and color, and by substrate, *A. choisyi* preferring, in general, looser sandy soils (which might also be inferred from label data; when commented upon, *A. choisyi* is said to occur in sandy or silty stream-side soils). Jan Saunders (pers. comm.) also noted that these two taxa appear distinct in the field in South America, *A. choisyi* being much more "ground-hugging" than *A. incarnata*, the stems of which appear more nearly procumbent.

Wedelia cristata is apparently a fruit form of var. *incarnata* having an overly enlarged ventrodorsal medial ridge, otherwise it differs little, if at all, from typical elements of the latter.

ALLIONIA INCARNATA L. var. *NUDATA* (Standl.) Munz

Wedelia incarnata (L.) Kuntze subsp. *nudata* Standl., Contr. U.S. Natl. Herb. 12:334. 1909. *Wedeliella incarnata* (L.) Cockerell subsp. (?) *nudata* (Standl.) Cockerell, Torreya 9:167. 1909. *Allionia incarnata* L. var. *nudata* (Standl.) Munz, *California Fl.* 391. 1959. TYPE: U.S.A. California: Coyote Canyon, ca. 1540 m, 1902, *E. Hall 2799* (HOLOTYPE: UC!).

Allionia malacoides Benth., *Bot. Voy. Sulphur* 44. 1844. TYPE: MEXICO. Baja Calif.: w/o locality, 1836-1842, *Barclay & Hinds s.n.* (HOLOTYPE: BM).

This taxon was apparently first described (at the species level) by Bentham in 1844, from material collected in Baja California, as noted in the above synonymy. It is largely distinguished from the allopatric var. *villosa* by its habit (seemingly annual or weakly perennial, the leaves relatively remote) and small perianths.

ALLIONIA INCARNATA L. var. **VILLOSA** (Standl.) B.L. Turner, *comb. nov.* BASIONYM: *Wedelia incarnata* (L.) Kuntze subsp. *villosa* Standl., Contr. U.S. Natl. Herb. 12:333. 1909. *Wedeliella incarnata* (L.) Cockerell var. (?) *villosa* (Standl.) Cockerell, Torreya 9:167. 1909. TYPE: U.S.A. Arizona: "Mesas and Foothills", 22 May 1881, *C.G. Pringle s.n.* (HOLOTYPE: MO; Isotypes: GH!,NY!).

This taxon is weakly differentiated from var. *incarnata* and is largely distinguished from the latter by its generally more robust habit, longer pedicels, and larger perianths with elongate anthers, as emphasized by Standley in his original description. Such large-flowered forms are seemingly restricted

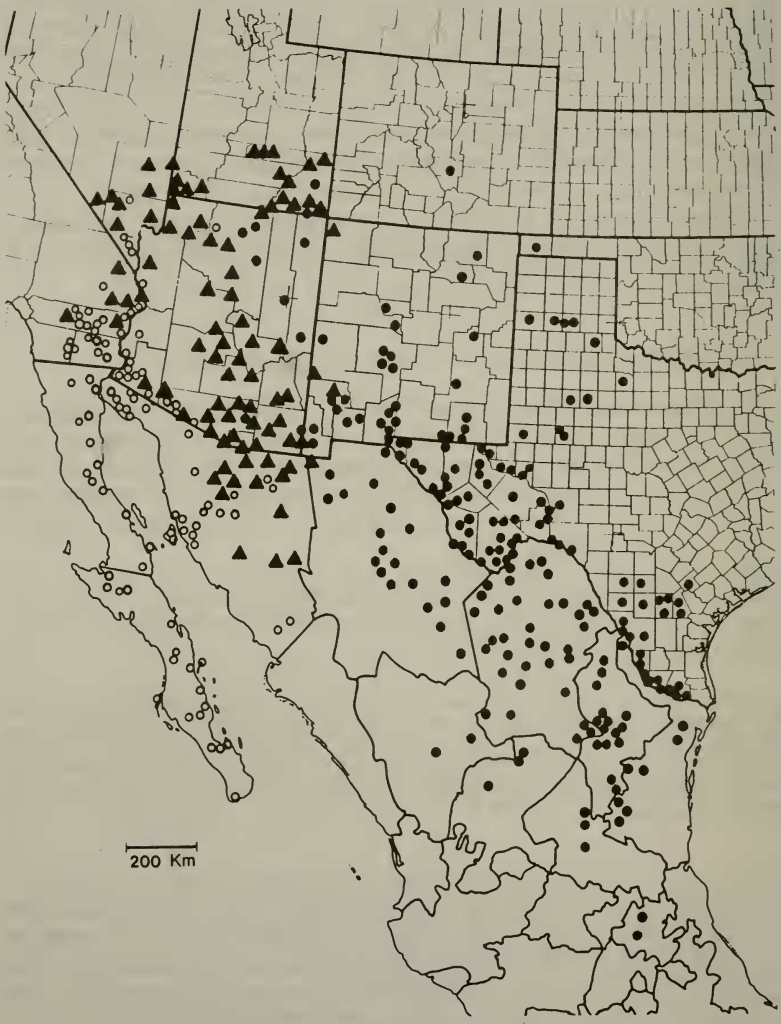

Figure 4. Distribution of *Allionia incarnata* in México and U.S.A.: var. *incarnata* (closed circles); var. *nudata* (open circles); and var. *villosa* (triangles).

to the northwestern portions of the Sonoran desert, standing between the small-flowered var. *nudata* to the west and the somewhat variable but also small-flowered var. *incarnata* to the east, as shown in Figure 2. Still, had the taxon not already been provided with a name, I would have not been hesitant to provide one since the combination of characters which mark it seem largely confined to Arizona and closely adjacent regions. Nevertheless, intermediates between var. *villosa* and var. *nudata* occur in regions of overlap, or near overlap.

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